

DRUMMING BEHAVIORS OF THREE PENNSYLVANIA STONEFLY (PLECOPTERA) SPECIES

DAVID D. ZEIGLER

Department of Biology, Southwest Texas State University, San Marcos, Texas 78666.
New address: Biology Department, Pembroke State University, Pembroke, North Carolina
28372.

Abstract.—Drumming behaviors of three central Pennsylvania stonefly species were described. Males of *Tallaperla maria* initially produced calls of a single scraping beat which shifted to a two-pulse scrape/beat call as signal exchanges with females continued. *Agnetina capitata* males produced a diphasic call that is the longest known in any stonefly species. The signals of *T. maria* and *Pteronarcys biloba* were compared to previous signal descriptions from geographically separate populations, and some intraspecific divergence of signal structure was found in these species.

Key Words: Plecoptera, stoneflies, drumming behavior, reproductive behavior, *Tallaperla*, *Pteronarcys*, *Agnetina*

Drumming behavior in stoneflies is a system of intersexual vibrational communication which aids in mate identification and location. The vibrational pulses that make up signals are typically produced when the insects strike or scrape the substratum with the posteroventral portion of the abdomen (Rupprecht 1967, Maketon and Stewart 1984). Drumming behavior was first quantified by Rupprecht in 1967. To date, numerous workers have described the signals of over 100 species (see Zeigler and Stewart 1987, Maketon and Stewart 1988 for literature citations). Continued descriptive work of this nature contributes to systematics (Zeigler and Stewart 1987) and to data banks which may help answer other assorted evolutionary questions, such as those raised by the current hypotheses concerning sexual selection's role in the divergence of reproductive behaviors (West-Eberhard 1984, Searcy and Andersson 1986). To elucidate

these and other evolutionary implications, more species and various populations within species must be studied. The present work describes drumming in three North American stonefly species and suggests some divergence of drumming between intraspecific populations.

MATERIALS AND METHODS

Virgin adults of two of the three species were obtained by rearing pre-emergent nymphs in styrofoam bait buckets. The nymphs were collected as follows: *Tallaperla maria* (Needham & Smith), Fisher Run, Columbia Co., PA, 12-V-1987; *Pteronarcys biloba* Newman, Fishing Crk., Columbia Co., PA, 18-V-1987. The adults of *Agnetina capitata* (Pictet) were collected in early May 1987 along the banks of the Susquehanna River at Danville, PA (Montour Co.). The presence of numerous emergent exuviae along the riverbank showed that *A.*

capitata nymphs were emerging from the Susquehanna and not from any nearby feeder streams.

All adults were allowed to adjust to lab temperature for at least one hour prior to recording. Drumming exchanges were recorded in stereo (male and female on separate channels) on cassette tapes using a recording setup similar to that described by Zeigler and Stewart (1985). All recordings of *T. maria* and *P. biloba* were of adults one to three days old. Signals were measured and analyzed using a Tektronix 5111 storage oscilloscope, and selected signals were photographed with a Nikon FG SLR camera.

RESULTS AND DISCUSSION

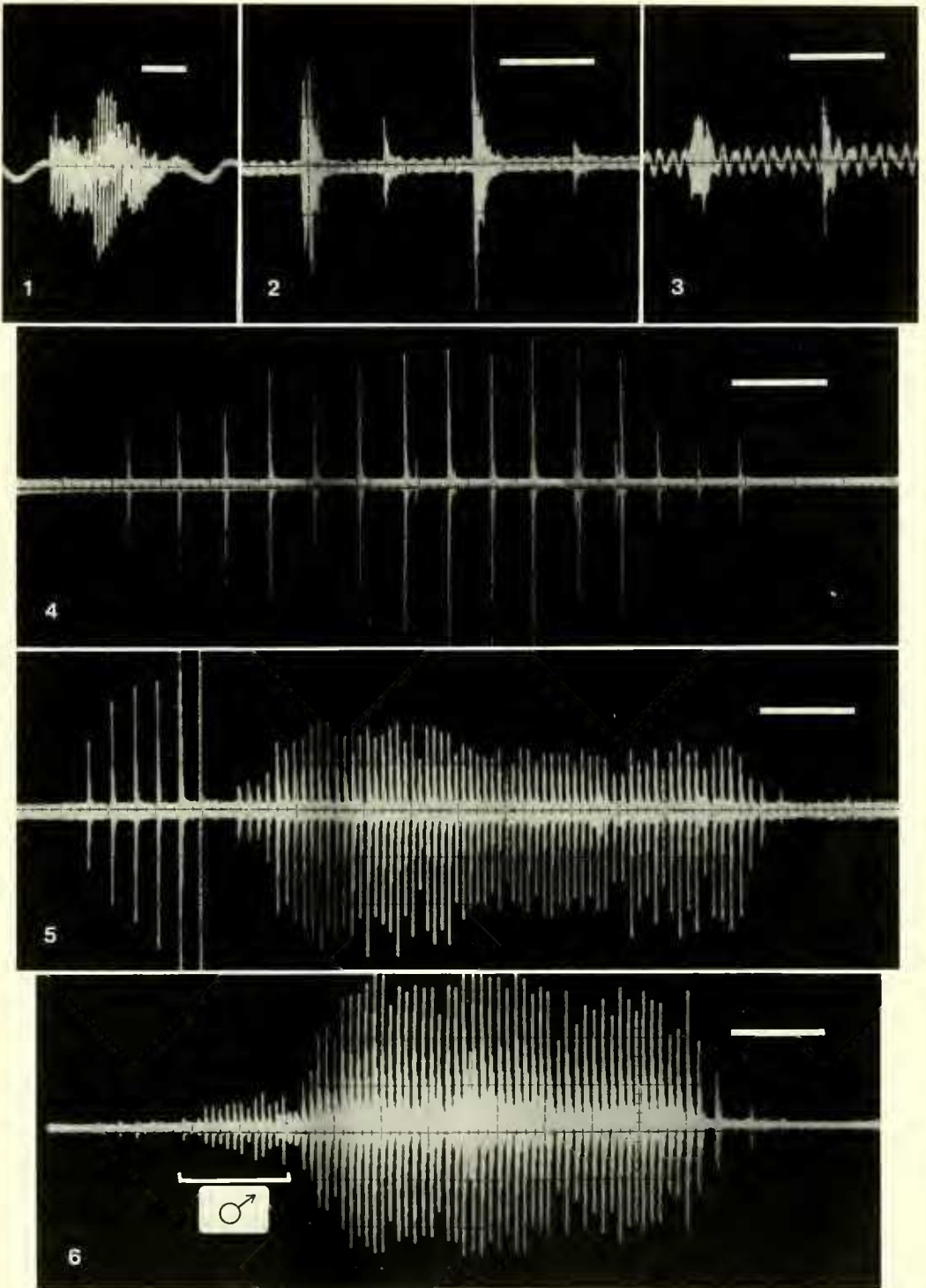
Tallaperla maria. — At 19–20°C males ($n = 7$) produced calls of a single scraping beat. Observations indicated that the scrapes were produced by curling the abdomen antero-ventrally to contact the substratum and then straightening the abdomen posteriorly thus scraping the abdomen tip across the substratum. The male's body rocked slightly in the posterior direction as the scrape was produced. The scrape tone averaged 596 ± 86 Hz with a duration of 47 ± 10 ms as measured on the oscilloscope screen (Fig. 1). However, scrape duration could have been less, because the residual ringing was impossible to distinguish from the scrape itself on oscilloscope tracings. When unanswered by a receptive female, male scrapes (calls) usually occurred in series of three to five calls. Within such a series, calls were separated by 1379 ± 175 ms.

Females ($n = 5$) produced answers consisting of a single abdomen/substratum beat which followed the male call after 178 ± 21 ms. After one to three of these simple exchanges, the males added a response scrape 190 ± 11 ms after the female's answer, and later exchanges evolved into four-part exchanges with a male call, female answer, male response, and female "response" (Fig. 2). In one pair, the male response was a simple beat rather than a scrape.

In three of the five pairs, the male switched to a different type of call in later exchanges within an exchange series. This call consisted of the initial scrape followed by a simple beat (Fig. 3). The scrape/beat interval was 245 ± 25 ms and the female answer typically followed in 181 ± 9 ms. In two of the five pairs, scrape/beat calls initiated a few three-part and even four-part exchanges as described above, but the majority of later exchanges consisted only of a male scrape/beat call and a female answer. Females were typically stationary between exchanges while males searched when not signalling.

Maketon and Stewart (1988) describe five "calls" from three males of another *T. maria* population in southwestern Virginia. They interpret the call as consisting of a series of scrapes similar to those noted for the Pennsylvania males when females were not answering. It seems likely that these Virginia calls were really a call series similar to those noted herein which would have broken down into single scrape calls if females had answered. Single scrape calls are described for *T. lobata* and *T. anna*, and another call series described in *T. elisa* (Maketon and Stewart 1988). Since no male/female exchanges were recorded for these species, it is impossible at this time to say if the scrape/beat calls produced by the Pennsylvania males late in exchange series are unique to this species or population. The intercall intervals in the call series of the Virginia population appear distinctly shorter than those noted for the Pennsylvania population (app. 450 ms vs. 1379 ± 175 ms, respectively) even allowing for the 4°C warmer recording temperatures for the Virginia population (see Zeigler and Stewart 1977 regarding drumming speed and temperature).

Pteronarcys biloba. — At 20°C, males ($n = 4$) produced calls of 12.5 ± 1.5 beats with beat intervals which were close to constant at 944 ± 53 ms. Only two answers from one female were recorded. These answers contained 9.5 ± 0.7 beats with relatively constant intervals of 869 ± 48 ms. These



Figs. 1–6. Oscillographs of drumming signals. 1, *Tallaperla maria*, male scrape call at 20°C (20 ms)*. 2, *Tallaperla maria*, four-part exchange at 20°C (200 ms)*. 3, *Tallaperla maria*, male scrape/beat call at 20°C (200 ms)*. 4, *Pteronarcys biloba*, overlapping male/female exchange at 20°C (1st female beat is seen after 7th male beat, some male and female beats overlap) (2000 ms)*. 5, *Agnatina capitata*, diphasic male call at 21°C (1000 ms)*. 6, *Agnatina capitata*, reinforcement event at 21°C (1000 ms)*. *Time indicated by white bar in upper right corner.

answers overlapped the male calls by five to six beats (Fig. 4). The overlap of call and answer is a relatively common occurrence in the genus *Pteronarcys* (Zeigler and Stewart 1987).

Stewart et al. (1982) describe drumming in a Tennessee population of *P. biloba*. They report a male call of seven to eight beats with beat intervals of 524 ± 46 ms. Recording temperature was not reported for the Tennessee population, so there is no way to guess whether a significant difference exists between the two populations in beat spacing. The difference in the number of beats per call seems significant (TN = 7.17 ± 0.8 ; PA = 12.5 ± 1.5), but the Tennessee data, taken from only one male, is insufficient for drawing a conclusion.

Agnatina capitata.—At 21–22°C six of seven males produced diphasic calls with 9.2 ± 2.6 beats in the first phase (Fig. 5). Within the first phase, beat intervals decreased from 256 ± 12 to 203 ± 22 ms. The interphase interval was 123 ± 19 ms. The second phase consisted of 68.9 ± 43.3 beats with intervals averaging 100 ± 14 ms, but typically starting and ending intervals averaged 110–120 ms while the central body of this phase consisted of 80–90 ms intervals. This diphasic call, which ranged up over 150 beats, is the longest male call, in terms of beat number, ever described in stoneflies.

One male produced monophasic calls that were indistinguishable from the first phase of the other six males' calls. This shortened call could have resulted because, in the initial exchange, the female answered before even this "first phase" was completed. Perhaps the male simply aborted his second phase due to the female's "premature" answer. The female also answered "early" in the second exchange, but not in the third and fourth where the male also delivered only a first phase type call. The longest calls recorded from other males (197 and 170 beats) were unanswered calls. It appears that males may stop signalling when the female

initiates her answer, otherwise delivering a longer call.

Females ($n = 3$) produced long answers of 185.4 ± 36.9 beats with relatively constant beat intervals of 82 ± 3 ms. Answers typically overlapped the last few beats of the male call. In two of three pairs, exchanges continued beyond the call and answer with what I am terming "reinforcement events." The male would overlap or follow closely the end of the female's answer with 12.9 ± 0.8 beats with intervals varying widely around 100 ms. These male beats would stimulate more female drumming in groups of 29.8 ± 11.4 beats with beat intervals similar to those in her answer. Reinforcement events (Fig. 6) usually numbered three to four per exchange and overlapped the previous event or followed after a pause of less than two seconds.

In the third pair, the male produced a signal of 121 ± 12.2 beats which overlapped or shortly followed the female's answer and terminated the exchange. Beat intervals in this signal were similar to those in the second phase of the call but with slightly longer beat intervals starting and ending this series. In two of the three pairs, males delivered a few (less than five) irregularly spaced "reinforcement beats" during the last half of the female's answer. These beats were delivered on the move (i.e. males did not cease their searching movements to produce these beats). The females remained stationary during and between exchanges. Males searched when not signaling, especially during the long female answers which could last as long as 25 seconds.

Maketon and Stewart (1984) and Graham (1983) report on drumming in populations of *Agnatina capitata* in Oklahoma and Wisconsin respectively. However, after a recent genus revision by Stark (1986), both previous studies were found to be on *A. flavescens* (K. W. Stewart and S. W. Szczytko personal communication). The present descriptions, then, are the first for *A. capitata*. Males in both populations of *A. flavescens*

produced a much shorter monophasic call. Since monophasic calls are generally believed to be the plesiomorphic condition (Zeigler and Stewart 1987), the extraordinary length and diphasic nature of the *A. capitata* calls appear to be apomorphic within the genus, although diphasic calls have apparently arisen separately in other genera and families (Zeigler and Stewart 1987). The reinforcement events noted above may likewise be apomorphic additions since they were not seen in the Oklahoma *A. flavescens* (no live male/female exchanges were recorded in the Wisconsin population), but conversely they could represent a shorter ancestral exchange with the initial diphasic call and long female answer being the apomorphic additions.

ACKNOWLEDGMENTS

I would like to acknowledge the cooperation of Dr. A. R. Mallard and the Communication Disorders Program of Southwest Texas State University for allowing me access to their Tektronix 5111 oscilloscope. I also thank Dr. Bill P. Stark for checking my species identifications.

LITERATURE CITED

- Graham, E. A. 1983. Drumming communication and pre-mating behavior of fourteen Nearctic stonefly (Plecoptera) species. M.S. Thesis. University of Wisconsin at Stevens Point. 79 pp.
- Maketon, M. and K. W. Stewart. 1984. Further studies of the drumming behavior of North American Perlidae (Plecoptera). *Ann. Entomol. Soc. Am.* 77: 770-778.
- . 1988. Patterns and evolution of drumming behavior in the stonefly families Perlidae and Pteronarcyidae. *Aquatic Insects* 10: 77-98.
- Rupprecht, R. 1967. Das Trommeln der Plecopteren. *Z. Vergl. Physiol.* 59: 38-71.
- Searcy, W. A. and M. Andersson. 1986. Sexual selection and the evolution of song. *Annu. Rev. Ecol. Syst.* 17: 507-533.
- Stark, B. P. 1986. The Nearctic species of *Agneta* (Plecoptera: Perlidae). *J. Kans. Entomol. Soc.* 59: 437-445.
- Stewart, K. W., S. W. Szczytko, and B. P. Stark. 1982. Drumming behavior of four species of North American Pteronarcyidae (Plecoptera): Dialects in Colorado and Alaska *Pteronarcella badia*. *Ann. Entomol. Soc. Am.* 75: 530-533.
- West-Eberhard, M. J. 1984. Sexual selection, competitive communication and species-specific signals in insects, pp. 283-324. *In* Lewis, T., ed., *Insect Communication*. Academic Press, New York.
- Zeigler, D. D. and K. W. Stewart. 1977. Drumming behavior of eleven Nearctic stonefly (Plecoptera) species. *Ann. Entomol. Soc. Am.* 70: 495-505.
- . 1985. Drumming behavior of five stonefly (Plecoptera) species from central and western North America. *Ann. Entomol. Soc. Am.* 78: 717-722.
- . 1987. Behavioral characters with systematic potential in stoneflies (Plecoptera). *Proc. Entomol. Soc. Wash.* 89: 794-802.